5. Palpi slightly longer than proboscis, densely hairy apically. Coxite more than twice as long as broad; basal lobe separated only towards the tip ..... *frenchi.*
Palpi slightly shorter than proboscis, with scanty and relatively short hairs. Coxite only about twice as long as broad; basal lobe is large, well separated and reaching nearly to the tip of the coxite ..... *hilli.*

Adult Females.

1. Proboscis pale beneath ..... *inconspicua.*
Proboscis black beneath 2
2. Tarsi entirely dark 3
Last segments of tarsi with pale reflections 4
3. Vertex with pale scales ..... *littleri.*
Upright scales on vertex dark ..... *frenchi atritarsalis.*
4. Base of tarsal segments with pale scales ..... *victoriensis.*
Base of tarsal segments without pale scales 5
5. Upright scales on vertex mostly pale. Venter usually with more or less conspicuous median patches of black scales ..... *hilli.*
Upright scales on vertex mostly dark. Venter pale scaled ..... *frenchi.*

Larvae (fourth stage).

1. Hair tuft near the middle of siphon ..... *littleri.*
Hair tuft at base of siphon 2
2. Pecten consisting of spine-like teeth 3
Pecten consists of a row of hairs 4
3. Larva milky-white in colour. Siphon tapering, anal papillae very long .... *victoriensis.*
Larva brown. Siphon slightly swollen in middle. Anal papillae short .. *inconspicua.*
4. Siphonal tuft with two branches ..... *hilli.*
Siphonal tuft of single hair ..... *frenchi.*

Description of Species.

Subgenus Neotheobaldia, n. subgen.

Theobaldia hilli Edwards.

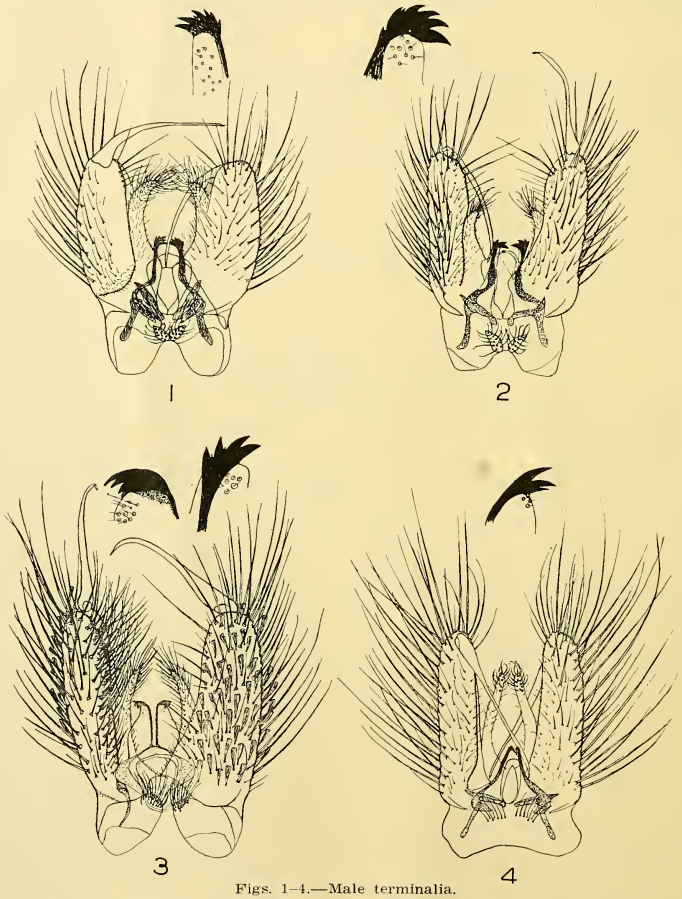
Edwards, F. W., 1926, *Bull. Ent. Res.*, 17: 111.

Type.—The type series from Beaconsfield, Victoria (6.XI and 8.XII.1923), is in the British Museum.

Distinctive Characters.—The Male. The upright scales on the vertex are pale becoming dark towards the neck. The proboscis and palpi are clothed with blackish scales with violet reflections. The palpi are slightly shorter than the proboscis; the apex of the shaft and the last two segments bear scanty and relatively short hairs; the terminal segment is about half as long as the penultimate. The thorax is brown with pale golden scales, which are rather larger and lighter than those of *T. frenchi.* The bristles are dark brown. The anterior pronotal lobe has three-four strong black bristles, several shorter pale golden ones, and a few narrow curved scales. The posterior pronotum bears narrow curved scales and four or five pale golden strong proepimeral bristles. The scutellum has five-seven strong black border bristles on each lobe. There are two pale spiracular bristles. The lower part of the sternopleura bears a long strong bristle and, below this, one or two shorter ones, several short fine ones and pale scales. The mesepimeron has a patch of pale scales and short bristles towards the middle; there are two strong bristles (the upper is shorter) on the lower part. The legs are black-scaled with conspicuous knee spots; the femora are pale beneath; the ends of the tarsi have light brown or pale reflection. The wing length is 3·5–3·6 mm. The first to seventh tergites are black-scaled with violet reflection; the eighth has black and pale scales. The colour of the venter is variable; usually the first to fourth sternites are black-scaled; the fifth to seventh have pale scales apically and these extend forward progressively so that the seventh sternite may have only a median patch of black scales; the eighth is black-scaled. But in some specimens the venter is pale with more or less conspicuous median patches of black scales on all sternites. The hypopygium (Fig. 1): The coxites are relatively short, being only about twice as long as broad. The basal lobe is large, well separated, and reaches nearly to the tip of the coxite; its tip has dense, long curved hairs. The aedeagus is rather large and strongly chitinized with four strong teeth and four shorter ones; on

the distal end there are about thirteen fine hairs. The lobes of the ninth tergite are prominent, with 9–10 curved hairs.

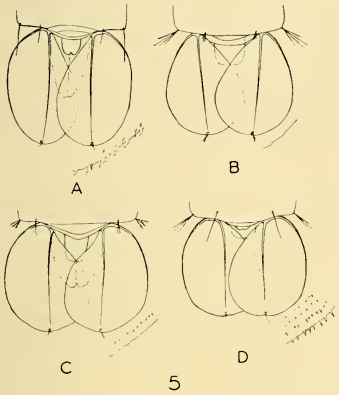
The females are similar to the males but differ as follows: The upright scales on the vertex are usually darker than in the male; in some specimens they are almost black. The last two segments of the tarsi are pale. Wing length is 3·5–3·8 mm. The upper fork cell is four times as long as its stem. The tergites are black-scaled with violet reflections; the fifth-seventh tergites have some pale scales on their apical corners. The venter is pale with, or without, median patches of black scales.



Figs. 1–4.—Male terminalia.
1, *T. hilli*; 2, *T. frenchi*; 3, *T. victoriensis*; 4, *T. littleri*.

The Pupa. This is milky-white with black hairs. The trumpet is short, with a large and very oblique opening, the margin of which is fringed. Seta A of the VIII segment of abdomen has four to six branches. The paddle (Fig. 5, B) is broadly oval with a smooth margin. At the tip of the midrib there are two setae, one very small and single, the other about three times as long and consisting of three or four branches.

The Larva. The fourth stage larva (Fig. 6) is milky-white in colour with black setae. The head is not very large; it is rounded, pale and almost transparent; the antennae have the subapical hairs slightly removed from the tip; the tuft consists of



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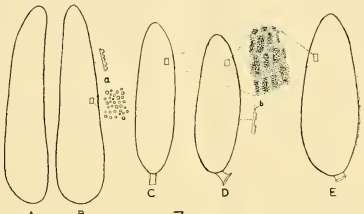

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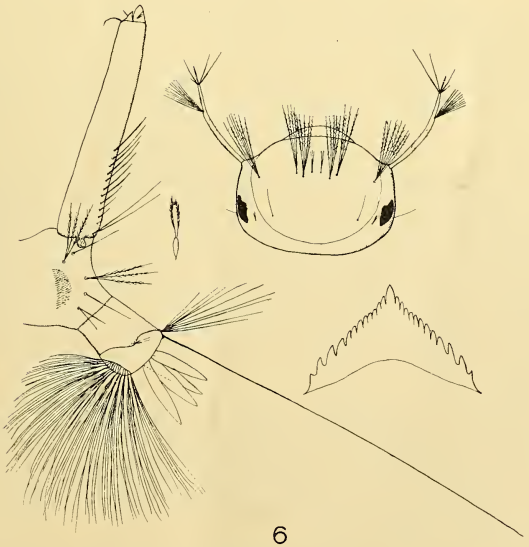

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Figs. 5–7.

5, Paddle of pupa: A, *T. littleri*; B, *T. hilli*; C, *T. victoriensis*; D, *T. inconspicua*. 6, *T. hilli* Edw. Head, terminal segments and mentum of larva. 7, Eggs of *Theobaldia*. A, B, *T. inconspicua* (two views); C, *T. hilli*; D, *T. frenchi*; E, *T. victoriensis*. *a* and *b* show the structure of the exochorion.

non-plumose hairs. The anterior frontal setae have three-five branches, the inner frontal four-six, middle frontal three-four, and the outer frontal five-eight. The sutural seta (*e*) is single, and the trans-sutural (*f*), which is one-third to one-half the length of

(c), has two-three branches. Prothoracic chaetotaxy: The first, second, fourth, fifth and sixth are single, the third has two-three branches, the seventh has two branches, and the eighth is a single minute tuft with about six branches. Abdomen: The hairs on segments I–VIII are short except for three lateral hairs on the first segment and a single lateral hair on the following five. The pentad hairs on the eighth segment: α usually has three branches, rarely four, β is single, γ has three plumose branches, δ is single and ϵ has two to three simple branches. There are about 90 comb teeth forming a large triangular patch. The inner dorsal brush consists of nine to eleven branches and a single long outer hair. The ventral brush has twelve to fourteen tufts. The anal papillae are pointed and of about the same length as the saddle. The saddle tuft is short with three or four branches. The siphonal index is 5·0–5·4. The siphon has a tuft of two hairs at the base. The pecten consists of a row of seven to eleven hairs.

The eggs (Fig. 7, c) are elongate-oval, silvery in colour, with a black base and a short transparent stem. The egg is about 0·88 mm. long with an index of about 4·3.

Distribution.—A total of 50♂♂ and 80♀♀ have been examined from the following localities: Ringwood, Christmas Hills, Beaconsfield, Healesville, Head of Cement Creek, Acheron River, Grace Burn Creek, Nyora, Tarra Valley Park, Stony Creek (Gippsland), Franklin River (N. Dobrotworsky), Trafalgar South, Upper Pakenham, Thompson, Tarago River, Dollar (near Meeniyan), Boolarra, Mirboo, Gembrook (A. Neboiss). *T. hilli* is confined to Victoria.

Theobaldia frenchi Theobald.

Culex frenchi Theobald, *Mon. Cul.*, 2: 66 (1901).

Type.—The type series of four females from Victoria (locality not stated) are in the British Museum.

The male was described by F. W. Edwards (1926) from Sassafras, Victoria.

Distinctive Characters.—The Male. Most of the upright scales on the vertex are dark. The palpi are slightly longer than the proboscis. Apically the shaft and the last two segments have dense, long hairs. The last segment is about half as long as the penultimate. The palpi and the proboscis are clothed with dark brown scales. The thorax is reddish and is clothed with pale golden scales; the bristles are black. The anterior pronotal lobes have two or three black bristles, some pale golden ones and a few narrow pale scales. The posterior pronotal lobes have a few narrow pale scales and four-five dark proepimeral bristles. There are one or two spiracular bristles. There are six-seven border bristles on each lobe of the scutellum. The sternopleura has, on the lower part, a patch of scales, a few pale hairs, one dark strong bristle and a second shorter one below. There are two lower mesepimeral bristles; the middle part of the mesepimeron has a patch of scales. The legs are clothed with dark brown scales; the tarsi are pale apically.

The abdomen is clothed dorsally with black scales, except the last segment, which has pale golden scales; the venter is clothed with pale, or black and pale scales. Hypopygium (Fig. 2*): Each lobe of the ninth tergite has a patch of nine-fifteen curved hairs. The coxite is more than twice as long as broad; the basal lobe is about two-thirds the length of the coxite; it is separated only towards the tip, which bears a tuft of rather short hairs. The aedeagus is rather large and strongly chitinized, with four large and three small teeth.

The female is similar to the male, but differs as follows: The anterior pronotal lobes have four-five strong black bristles. Each lobe of the scutellum has about eight

* It will be noted that this figure is very similar to that given by Lee (1937, p. 296, Text-fig. 3) for *T. weindorferi*. Through the courtesy of the Division of Entomology, C.S.I.R.O., I have been able to examine the type of *T. weindorferi*; the mounted terminalia correspond exactly with Lee's Text-figure 4, labelled *T. frenchi*. There can be no doubt that in Lee's paper, Text-figures 3 and 4 were transposed. Text-fig. 3 should refer to *T. frenchi* and Text-fig. 4 to *T. weindorferi*.

border bristles. The patch of scales on the pleurae is more distinct. The legs are darker, almost black above; the femora and tibia are pale beneath. There are conspicuous knee spots of pale scales; the last three segments of the tarsi are pale. The venter is pale. Wing length is 3·8–5·0 mm. The upper fork cell is 3·0–4·5 times the length of the stem.

The Pupa. This is very similar to the pupa of *T. hilli.*

The Larva. The fourth stage larva is similar to that of *T. hilli* but can be distinguished from it as follows: The frontal setae are more branched, the pentad hair γ on the eighth abdominal segment usually has 4–5 branches, the basal siphonal tuft is represented by a single hair. (In *T. hilli* the basal tuft always has two branches.)

The eggs (Fig. 7, D) are similar to those of *T. hilli*; they are about 0·7 mm. long, with an index of 3·4–3·5.

Distribution.—A total of 15♂♂ and 120♀♀ were examined from the following localities: Sherbrooke, Kalista, Grace Burn Creek, Healesville, Head of Cement Creek, Tarra Valley Park (N. Dobrotworsky), Menzies Creek, Tanjil South (A. Neboiss). As far as is known, *T. frenchi* is confined to Victoria.

THEOBALDIA FRENCHI ATRITARSALIS, n. subsp.

This subspecies is clearly distinguished from the type by its general darker colour; the thorax is brown, the proboscis, the palps and the legs are clothed with almost black scales; the legs also are dark apically. The male palpi are even more hairy than those of the type, and the shaft apically has about thirty long hairs. The male genitalia are identical with that of the type.

The pupa, larva and eggs are identical with those of the type.

Types.—The holotype male, allotype female and a paratype series from Stony Creek (Gippsland) are in the collection of the National Museum, Melbourne.

Distribution.—A total of 5♂♂ and 44♀♀ have been examined from the following localities: Stony Creek (Gippsland), Franklin River, Kalimna, Tarra Valley Park (N. Dobrotworsky), Boolarra, Mirboo North, Thompson, Hiawatha, Tyres River, Gould (A. Neboiss).

Subgenus CULICELLA Felt.

THEOBALDIA VICTORIENSIS, n. sp.

Types.—The holotype male and allotype female were bred from larvae collected at Ringwood, Victoria, 3.8.52. These, together with a paratype series of 10♂♂ (three from Ringwood 3.8.52 with associated larval and pupal skins, five from Tarra Valley Park 5.5.53, two from Boolarra 8.5.53) and 10♀♀ (six from Ringwood 1.1.52, 7.1.53, 1.3.53 and 6.4.53, two with associated larval and pupal skins, two from Tarra Valley Park 5.3.53, two from Healesville 30.1.53), are in the collection of the National Museum, Melbourne.

Description of Adult.—Holotype ♂. The head scales are pale; a few upright ones become dark toward the neck. The palpi are as long as the proboscis. The shaft bears about 10 long hairs; the last two segments have long but relatively sparse hairs; the terminal segment is about half as long as the penultimate. The proboscis and the palpi are clothed with black scales with violet reflections. The thorax is brown, with pale golden scales; the small bristles are pale, the strong ones are pale at the base and dark at the end. The anterior pronotal lobe has pale golden bristles and a few narrow curved scales; the posterior pronotum has a number of curved scales and five pale golden proepimeral bristles. There are two fine pale spiracular bristles. The scutellum has narrow curved pale scales, with four-five border bristles on the lateral lobe and eight on the central. On the lower part of the sternopleura there are fine hairs, a few narrow scales, one strong bristle and several shorter ones. The mesepimeron has a number of fine hairs towards the middle and two strong lower mesepimeral bristles (upper is shorter). The legs are dark brown with inconspicuous knee spots. The tarsi: the second to fourth segments of the forelegs and the first to third of the mid- and hindlegs are pale at the base; the last two segments of the tarsi are covered with pale scales. The wing length is 4 mm. The abdomen is unbanded. The tergites are clothed with black scales with violet reflections and pale hairs. The apical border

of the eighth tergite has pale scales. The venter is also black-scaled but the fourth-seventh sternites have pale scales apically. The hypopygium (Fig. 3): The coxites have long pale goldish hairs, black scales dorsally, and dense pale goldish hairs ventrally on the inner face.

Paratypes ♂. The series of 10 paratype males differs from the type in colouring. The venter in some specimens is pale with large median patches of black scales. Each lobe of the ninth tergite has a patch of ten-twelve curved hairs. The coxites are more than twice as long as broad. The basal lobes of the coxites are hairy; they are about two-thirds of the length of the coxite and are separated from them only at the tip, which bears a tuft of long hairs. Wing 4·0–4·1 mm.

Allotype ♀. This differs from the holotype as follows: The forked upright scales on the head are pale only in front and gradually become black towards the neck. The strong bristles on the thorax are black. The anterior pronotal lobes have three strong black bristles, several golden ones and a few narrow scales. There are three pale spiracular bristles. The sternopleura has one strong bristle and several shorter ones. The mesepimeron has a patch of hairs towards the middle and one strong and three short lower mesepimeral bristles. The legs are almost black, with violet reflections. There are conspicuous knee spots. The first three segments of the tarsi have pale basal rings; the fourth and fifth are pale; the third segment of the hind-tarsi is also pale apically. Wing: The upper fork-cell is 3·8 times as long as its stem; wing length is 4·7 mm. The venter is pale-scaled with inconspicuous median patches of black scales.

Paratype ♀. The series of 10 paratype females do not show much variation; the upright scales on the head are predominantly pale in some specimens and become dark only towards the neck. The mesepimeron has a patch of hair, a few narrow scales and two-three strong lower mesepimeral bristles. The length of wing is 3·8–5·1 mm.; the upper fork cell is three-four times as long as its stem. The median patches of black scales on the venter may be large.

The Pupa. The trumpet is similar to that of *T. hilli.* Seta A of VIII abdominal segment has three or four plumose branches. The paddle (Fig. 5, C) is broadly oval with a smooth margin and a few minute denticles slightly removed from the margin. At the tip of the midrib there are two setae; one is small and single, the other is twice as long and usually two-branched.

The Larva. The fourth-stage larva (Fig. 8) is milky-white with black setae. The head is large, oval, pale, almost transparent and with very small eyes. The antennae are long, thin and curved, with a tuft of fourteen-sixteen slightly plumose hairs. The anterior frontal setae are single or double, the inner frontal consist of four to five hairs, the middle frontal of two, and the outer frontal of six-seven. All these except the anterior frontal are plumose. The sutural seta (*e*) has two branches and the trans-sutural (*f*), which is half as long, has two-three branches. Prothoracic chaetotaxy: The third seta is single or two-branched, the fourth is short and has two or three branches, the fifth and sixth are single, the seventh has three branches, and the eighth is minute with about four branches. Abdomen: The hairs on segments I–VIII are very short, except three lateral ones on the first segment and a single lateral hair on segments II–VI. The pentad hairs on segment VIII: α has four-five slightly plumose branches, β is single, γ has two-three plumose branches, δ is single, and ϵ has two branches. The comb teeth form a large patch. The inner dorsal brush consists of seven-eight tufted hairs and a single long outer hair. The ventral brush has about fifteen tufts. The anal papillae are slender, pointed and twice the length of the saddle. The saddle tuft, which has two-five branches, is small. The siphon is long, slender, pale at base but gradually becoming brown apically. The siphonal tuft is at the base and has two branches. The siphon index is 6·3–6·8. The pecten consists of ten to thirteen spine-like teeth.

The eggs (Fig. 7, E) are similar to those of *T. hilli,* but have more pointed ends; the index is 2·8–3·2, the length 0·8 mm.

Distribution.—Besides the type series, a total of 10♂♂ and 70♀♀ have been examined from the following localities: Ringwood, Christmas Hills, Healesville, Grace Burn Creek, Head of Cement Creek, Meeniyan, Tarra Valley Park, Franklin River, Nyora, Stony Creek (Gippsland), (N. Dobrotworsky), Boolarra, Thompson, Upper Pakenham, Menzies Creek, Kinglake, Dollar (near Meeniyan) (A. Neboiss).

THEOBALDIA INCONSPICUA Lee.

Lee, D. J., 1937. PROC. LINN. SOC. N.S.W., lxii: 294–298.

Type.—The type series from Tinderry and Mittagong. Holotype and allotype are in the Museum of the Commonwealth Scientific and Industrial Research Organization, Canberra.

As the adults and larva were carefully described by Lee (1937) only a brief description is given here.

Adult. The upright scales on the vertex are dark brown, some in front are pale. The proboscis is dark brown above and pale beneath. The male palpi are as long as the proboscis. The penultimate segment has scanty and relatively short hairs; the last has only a few long hairs on the inner side at the basal part. The last two segments of the palpi, in living specimens, are bent backwards. The anterior and posterior pronotal lobes are devoid of scales. The tarsi are entirely dark. Ventrally the abdomen is clothed with dark scales basally becoming pale goldish apically. The male hypopygium: The coxites taper and are more than twice as long as broad; the basal lobes are very small and imperfectly separated from the coxites. The aedeagus has three large teeth.

The pupa is brown; the trumpet is short with a very large and oblique opening. Seta A of the eighth abdominal segment has two or three branches. The paddle (Fig. 5, D) is oval, with minute denticles on its surface and larger ones at the margin. At the tip of the midrib there are two setae; one is minute and single, the other is single or two-branched.

The Larva. The fourth-stage larva is brown. The head is large; the antennae are long. The anterior and middle frontal setae are single, the inner frontal seta consists of two branches. Prothoracic chaetotaxy: The first, second, fifth, sixth and eighth setae are single; the third, fourth and seventh setae each consists of two branches. The hairs on the abdomen are well developed. The eighth abdominal segment: The comb teeth form a large patch; the siphon is long, slightly swollen in the middle, with an index 5·0–5·5. There is a single hair at the base of the siphon. The pecten conists of 9–10 serrate teeth.

The eggs (Fig. 7, A, B) are deposited in rafts, which are rounded or oval in shape with raised margins, and look like a basket. The egg rafts, which contain up to 217 eggs, exceed 4 mm. × 2 mm. The eggs are black, thick at one end and tapering to the other; the length of egg is 0·9–1·0 mm., with index of about 4·0.

Distribution.—A total of 30♂♂ and 40♀♀ have been examined from the following localities: Ringwood, Melbourne, Kalista, Sherbrooke, Healesville, Tarra Valley Park, Kalimna, Violet Town (N. Dobrotworsky), Shoreham (F. Drummond), Menzies Creek (A. Neboiss). The species also occurs in New South Wales (Lee, 1937) and Tasmania (Sulfur Creek, K. W. Dillon).

Subgenus AUSTROTHEOBALDIA, n. subg.

THEOBALDIA LITTLERI Taylor.

Chrysoconops littleri Taylor, 1913–1914, *Trans. Ent. Soc. Lond.*, p. 702. *Theobaldia littleri* Taylor, Lee, 1937, PROC. LINN. SOC. N.S.W., lxii: 295.

Type.—The type female, from Mt. Arthur near Launceston, is in the School of Tropical Medicine, Sydney. The presumed males, described by Lee, one from Barrington Tops, N.S.W., another from National Park, N.S.W., are in the Macleay Museum.

Distinctive Characters.—Adult. The male. The upright scales on the head are pale. The palpi are slightly shorter than the proboscis; the shaft has six to eight long apical hairs; the last segment, which is about twice as long as the penultimate, bears

dense long hairs. The palps and the proboscis are clothed with brown scales. The thorax is brown and bears pale golden scales; the strong bristles are black, the short ones, pale golden. The anterior pronotal lobe has three to four strong black bristles, several pale shorter ones and narrow curved scales. The posterior pronotum has narrow curved scales, and five-six pale golden proepimeral bristles. The scutellum has four-six border bristles on the lateral lobe and six on the central. There are three very fine spiracular bristles. The postspiracular area has four-five minute scales. The sternopleura has one strong bristle, several shorter ones and flat pale scales. The mesepimeron has a patch of flat scales towards the middle, and two strong and a few short lower mesepimeral bristles. The legs are black without knee spots; the femora are pale beneath. The tarsi are entirely dark brown. Wing length is 3·8–4·0 mm.

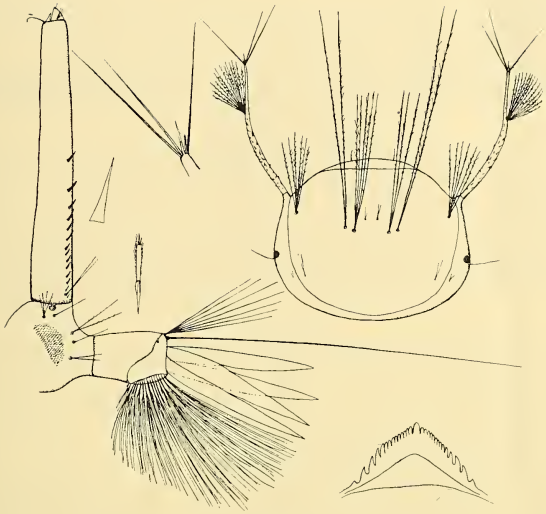
The wing veins are covered with brown scales. The underside of the subcostal vein has hairs and some narrow scales proximal to the humeral cross-vein. The upper corner of the alula has four-five scales. The abdomen: 1st-7th tergites are black with violet reflections and pale bristles; the VIIIth tergite is clothed with a mixture of black and light brown scales. The venter is light brown, with or without lateral triangular areas of brown and black scales; the VIIIth sternite is entirely black-scaled. The hypopygium (Fig. 4): The coxites are almost three times as long as broad. The basal lobes are about two-thirds of the length of the coxite and are separated for nearly their whole length; they bear rather strong spines. The lobes of the ninth tergite are not prominent; each bears four-seven bristles. The aedeagus is rather large and strongly chitinized, with three strong teeth and, under them, a few fine bristles.

The female differs from the male as follows: The anterior pronotal lobe has about six strong black bristles. There are three strong black proepimeral bristles and a couple of shorter ones. The scutellum has six black bristles on the lateral lobe and seven on the central one. The postspiracular area has seven to eight minute scales. The sternopleura has one strong bristle and a shorter one. Wing length is 3·8–4·5 mm. The upper fork cell is 3·2–4·0 times as long as its stem. The upper corner of the alula has about eight scales. The fifth-seventh tergites have some pale brownish scales laterally. The venter is pale with light brown reflections.

The Pupa. The trumpet is short, with a large and very oblique opening, the margin of which is fringed. Seta A of the eighth abdominal sternite is single. The paddle (Fig. 5, A) is oval with minute denticles on its margin; at the tip of the midrib there are two single setae.

The Larva. The fourth-stage larva (Fig. 9) is reddish-brown; all the hairs are non-plumose. The head is broad and pale; the antennae are long, thin and curved, with a tuft of about seven hairs. The anterior frontal setae are single, the inner frontal have two or three long branches, the mid-frontal are single and longer than the inner frontal, and the outer frontal has two branches. The sutural and the trans-sutural setae (*e* and *f*) have two-three branches. The mental plate has a central tooth and about ten lateral teeth. The thorax: Prothoracic chaetotaxy: the third, fourth and seventh have two branches; the remaining setae are single. The abdomen: The hairs on segments I-VII are well developed; the lateral hairs consist of two or three branches. The pentad hairs on the eighth segment are long: α has eight or nine branches, β is single, γ has three to five branches, δ is single, and ϵ has three branches. The lateral comb consists of sixteen-thirty small scales in a basal row, and eight-fifteen long scales forming a patch. The inner dorsal brush has five to six branches and one long and one or two short outer hairs. The ventral brush has ten or eleven tufts. The anal papillae are narrow and usually equal in length to the saddle. The saddle hair is single and as long as the saddle. The siphon is long and slender, with an index of about seven. The hair tuft consists of one or two hairs about half the way along the siphon; there is no basal hair tuft. The pecten, which does not reach the hair tuft, consists of 13–14 small triangular teeth.

The First-stage Larva. The position of the siphonal hair tuft (a single hair) is variable; in some specimens it is near the middle of the siphon, as in the fourth-stage larva, but sometimes it arises closer to the base.



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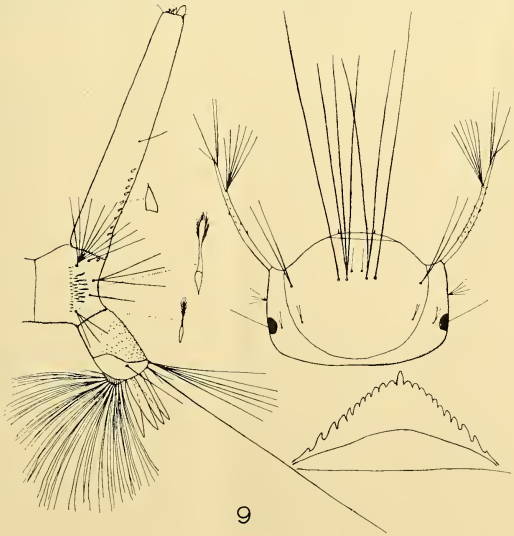

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Figs. 8–9.

8, *T. victoriensis*, n. sp. Head, terminal segments and mentum of larva. 9, *T. littleri* Tayl. Head, terminal segments and mentum of larva.

In several species of *Theobaldia*, e.g. *T. inconspicua*, *T. victoriensis* and European forms, the siphonal tuft of the first instar larva lies some distance from the base, alongside the pecten. In the second and later instars it shifts to the typical basal position. In *T. littleri* the shift in position is in the opposite direction.

Distribution.—In Victoria *T. littleri* is known only from Sherbrooke Forest. It has also been recorded from Tasmania (Taylor, 1913) and New South Wales (Lee, 1937).

Acknowledgements.

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THE INHERITANCE OF INFLORESCENCE CHARACTERS IN *EUCALYPTUS*.

By L. D. Pryor.

(Eight Text-figures.)

[Read 30th June, 1954.]

Synopsis.

The inflorescence of *Eucalyptus* is considered to be a dichasium contracted to give the outward appearance of an umbel. Inflorescences of either 3 or 7 flowers are very common in the genus. The 7-flowered unit is found to be partially dominant to the 3-flowered cluster. Irregular combinations between 3 and 7 flowers sometimes occur in the F1 and often in segregates in later generations.

To understand the inheritance in hybrid combination of inflorescence characters in *Eucalyptus* it is necessary first to know the normal features of this structure in the genus. A review of the literature shows there is a good deal of confusion. This has persisted probably for three main reasons: firstly, because the method of ordinary herbarium preservation generally results in the blurring or loss of the characteristic arrangement by which the basic inflorescence pattern might be determined; secondly, special field collection and observation designed to reveal these characters is necessary to secure material which can be interpreted easily; and, thirdly, from the point of view of descriptive botanical work aimed mainly at systematic ends, it is of minor value in diagnosis to separate, in the description, an umbel from an "umbel-like" cyme, or a three-flowered umbel from a three-flowered cyme.

Review of Literature Relating to Eucalyptus.

Bentham (1863) simply regarded the flowers of *Eucalyptus* as "in umbels or heads . . . rarely reduced to a single sessile flower", and Mueller (1882) in "Eucalyptographia" briefly described the flowers as occurring "in single or paniculated umbels . . .".

Maiden (1924, I, 9) quotes Tate as saying, "the usual form of inflorescence is an umbel which by lengthening of the axis passes to a panicle or corymb". At the same time Maiden (ibid.) quotes Naudin, in particular with regard to a key for a group of some 50–60 species raised in France, in which he makes two contrasting groups, one having an inflorescence of "cymes or umbels", the other having panicles or corymbs; and later (VI, 446), Naudin's work is again quoted, in which in various groups of species he refers to the inflorescence as "cymes or three-flowered umbels" as opposed to "axillary umbels with three to eleven flowers".

The determination of the inflorescence as a cyme or an umbel is hampered in *Eucalyptus* by the fact that the bracts and bracteoles, if they do occur, have been found in few species and are very early deciduous. They are, however, present in at least some Corymbosae, and Maiden (ibid., VI, 467) found that with *E. ficifolia** "The bracts and bracteoles alternate, and they show six segments . . . each umbel shows seven buds, and it may be that one bracteole has aborted or it was so early deciduous that it was not seen". Maiden makes it clear, however, that he considers the matter inconclusive and that later study may elucidate matters with regard to the inflorescence. He says: "Doubtless botanists will give special attention to bracts and bracteoles in the future and may be able to offer useful generalization."

Blakely (1934) simply says that the flowers are "in umbels or heads, usually pedunculate, rarely reduced to a single sessile flower . . .".

Naudin's view has been renewed and developed, however, by Blake (1953) recently, in which he first comments on the inflorescence by saying that "the primitive unit of

* Nomenclature as in Blakely, "A Key to the Eucalypts".

inflorescence appears to be a three-flowered cyme pedunculate in the axils of the leaves of an ordinary vegetative twig. The cyme may be reduced to one or two flowers, but in most species it has been altered to an umbel of few or many flowers. In many species paniculate inflorescences have resulted from the shortening of the internodes of the twigs accompanied by reduction and finally the loss of the leaves at least in the upper part."

It will be noted in passing that this suggestion as to the origin of the paniculate inflorescence is the reverse of that suggested by Tate, recorded above. Blake goes on to say: "The primitive three-flowered cyme persists (or sometimes occurs as a result of secondary reduction?) as a regular feature of many quite dissimilar species . . . and is occasionally met with in many others; reduced cymes are usual in such unrelated species as *E. globulus* and *E. macrocarpa* . . . ." Blake's remark in parentheses is apparently the first suggestion that the three-flowered inflorescence of *Eucalyptus* is perhaps a reduced cyme.

Blake makes one other relevant note of interest in commenting on the inflorescence in Myrtaceae from a phylogenetic point of view. He points out that the characteristic inflorescence for two groups within the Myrtaceae, namely, the Myrteae and Metrosiderinae, is a more or less terminal, dichotomous (or trichotomous) cyme, particularly in the Australian-Malaysian region.

From the above it will be seen that there is considerable confusion of ideas as to how the inflorescence of *Eucalyptus* should be regarded.

The Inflorescence of Dicots.

It seems that study of the inflorescence has been impeded in various ways since the time of Linnaeus to the extent that the understanding of its structure has, in many cases, come much later than one might expect from the general development of botanical knowledge.

A recent paper by Rickett (1944) on the classification of inflorescences gives a thorough review of the position. He points out that views with regard to the nature of the inflorescence have varied considerably since the time of Linnaeus, and have been obscured at different times, particularly by philosophical treatment, such as resulted from Goethe's views. Amongst other things, this led to the use of the character of centrifugal and centripetal order of blooming as a basis in classification, whereas it has become clear that this is a matter of physiology rather than structure, and must be discarded as a basis of classification and understanding of inflorescence structure.

When progressive study of the inflorescence began to take place, this was finally summarized by Eichler, since when there has been further steady progress.

Rickett draws attention to the fact that, "In dealing with complex clusters it is noticeable how often one encounters a dichasial group of flowers as a sort of unit cluster, the entire inflorescence being composed of many such units variously related".

Rickett suggests that a dichasium be supposed as the simplest and most primitive form of inflorescence. "By dichasium", he says, "I use the word in its strict sense to mean a cluster formed by an apparent dichotomy beneath a terminal flower—in its simplest form consists of three flowers." Rickett further emphasizes that he does not imply that the simple dichasium is necessarily earlier in evolutionary history than the more complicated dichasium. The first inflorescence may already have been a much-branched system. The transition is equally easy in either direction. "From a primitive dichasium may be derived also without extensive changes, bostryches, cincinnae and the rest, and by shortening of the internodes, many of the 'umbellate' and 'capitate' clusters characteristic of Liliaceous and Cornaceous genera."

He says, further, that the dichasium might well be the basic inflorescence pattern of a very large number of dicots. As will be shown later, this suggestion has particular application in considering *Eucalyptus*. From an original dichasium he postulates the

steps in evolution of an apparently simple inflorescence from the primitive dichasial type to be perhaps as follows: (*a*) the limitation of an original dichasium to a few flowers; (*b*) grouping of branches bearing leaves and terminated by dichasia on a common axis—a grouping which involves the shortening of the branches and of the internodes between them; (*c*) reduction of leaves to bracts.

After discussing the way in which many "umbels" may arise from the dichasium, he says that "Since our terminology is to be used by systematists who cannot always postpone their conclusions for microscopic investigation, it would be wise to use the term 'umbel' for all clusters whose branches arise from a common point". But he adds in addition that where the structure of an "umbel" is understood, it might further be designated as sympodial or monopodial.

Of the many studies that have been made of inflorescences in different groups, it is interesting to note that of Woodson (1935), who postulated the dichasium as the starting point for inflorescences of the Apocynaceae, from which he was able to demonstrate how all the types of inflorescences found in that family might be derived.

The Basic Characters of the Eucalyptus *Inflorescence.*

From field observation of suitable material, particularly flower clusters soon after they have emerged from the two covering bracts, it is clear that the inflorescence of *Eucalyptus* is considerably more regular than has been thought. There are good reasons for supposing that while it has in many cases the outward appearance of an umbel, it is in fact a dichasium, in which the axes below the position of the bracteoles are extremely contracted or eliminated so that the true form is not at once apparent. It may well be postulated that there is a basic branching pattern in *Eucalyptus* perpetuated by buds which are decussate and opposite. This system, which may never have existed in the neutral state, is expressed in one form to give a leaf-bearing system, and in another to give a flower-bearing system.

Jacobs (n.d.) has shown how this is the basic pattern in the leaf-bearing system, where the leaves of *Eucalyptus*, while appearing alternate and two-ranked, are part of a modified decussate and opposite system of branching. In a parallel but alternative way it seems that the basic branching pattern has been modified to suit the flower-bearing structure so that a flower cluster with the form of an umbel has been derived from the basic branching which is decussate and opposite.

From the phylogenetic point of view it is interesting to note that a dichasial inflorescence at once fits the pattern of the Australian members of the groups Myrteae and Metrosiderinae, and makes *Eucalyptus* homologous with many members of these groups in this respect.

Angophora affords an interesting comparison. Bentham describes *Angophora* as having "flowers in umbel-like cymes arranged in terminal corymbs". The illustrations of *Angophora intermedia* (Fig. 1, *a*, *b*) make this quite plain, and the briefly persistent bracts and bracteoles clearly indicate that the inflorescence is a dichasium.

If it is supposed that the *Eucalyptus* flower clusters are derived phylogenetically by reduction from a preceding inflorescence which was an indefinitely prolonged dichasium, the number of flowers in each inflorescence at different degrees of reduction, assuming it is completely regularly branched, could be 1, 3, 15, 31, 63, 127, and so on, as shown in Figure 2, *c*.

If it is assumed that in some circumstances, however, reduced branching occurs at some stage (presumably due to crowding following contraction) by the elimination of one side of the dichotomous branching due to suppression of both buds facing each other from separate parts of the ramification across the now confined space, the numbers of flowers in the flower cluster could be 1, 3, 7, 11, 15, 23, 35, etc., arranged in the pattern as shown in Figure 2, *a* (the Xs show the suppressed buds).

As a further possibility, if, where, due to crowding in the same way, there is space for which two adjoining buds are competing, instead of both being suppressed as is supposed in the previous case, one has developed to fill the available space and

the other remained rudimentary, a pattern of numbers could be 1, 3, 7, 13, 21, 31, and so on, and the arrangement as shown in Figure 2, *b*.

It is of interest, then, to examine the inflorescences of various species to see how they conform with the numbers possible under various kinds of dichasial branching if unmodified or, alternatively, if modified in the two simple ways set out above. It will be noticed that the numbers 15 and 31 can be derived in two ways. The likely numbers which could therefore result from a regular branching are 1, 3, 7, 11, 15 and 31, with a somewhat lesser frequency of 21 and 23.

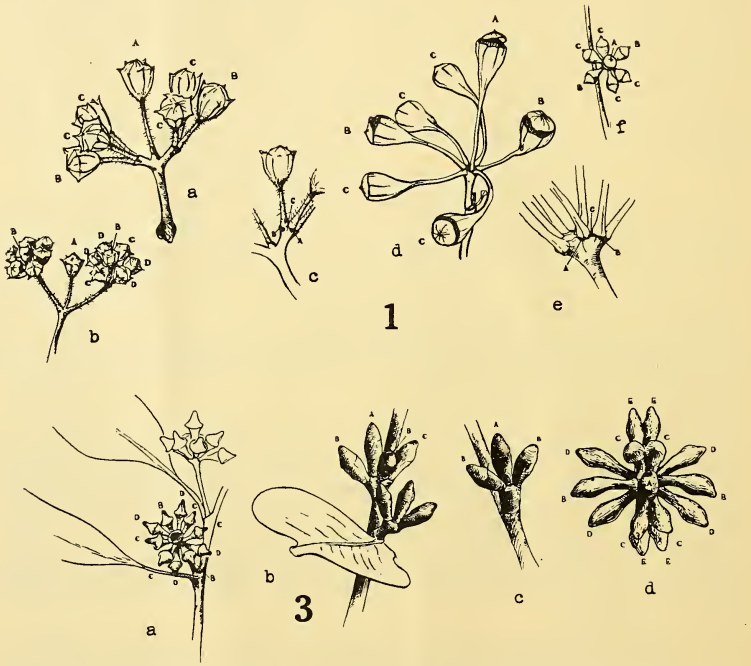

Fig. 1.—*a*, *b*, Showing two variations of the dichasium of *Angophora intermedia*. It will be noted that unlike Eucalyptus the axis below the bracts persists in some degree. *c*, Showing the bracteole scars; A, B, C, corresponding with successive branches of the dichasium. *d*, *e*, *E. ficifolia*: *d*, The typical seven-flowered dichasium showing the branching order A, B, C; *e*. Showing the bracteole scars which correspond with dichasial branching, A. B, C. *f*, *E. Macarthuri*, a typical seven-flowered dichasium. The branching order is shown by the letters A to C.

Fig. 3.—*a*, *Eucalyptus macrorrhyncha*, a species which often has eleven-flowered inflorescences; branching order is indicated from A to D. *b*, *c*, A segregate from *E. elaeophora* (seven-flowered), *E. viminalis* (three-flowered). Note in *b* the three-flowered cyme produced below the irregular four-flowered cyme in the same axil. *d*, *E. pauciflora* showing a typical fifteen-flowered dichasium with the order of branching indicated by the letters A to E.

It must be remembered that, after emergence, the buds are very easily lost from the inflorescence from failure to grow or by accident, and therefore the material must be carefully examined. If branching is regular, it is likely that a regular geometric pattern can be seen in the flower cluster if examined at a suitable stage. There seems no reason to assume that regular branching will occur indefinitely. One branch of a